Antagonistic coevolution between multiple quantitative traits: Matching dynamics can arise from difference interactions

Masato Yamamichi[1,*], Kelsey Lyberger[2], Swati Patel[3]

1) Department of General Systems Studies, University of Tokyo, Tokyo, Japan

2) Department of Evolution and Ecology, University of California, Davis, Davis, California

3) Department of Mathematics, Tulane University, New Orleans, Louisiana

[*]Corresponding author: c-yamamichi@mail.ecc.u-tokyo.ac.jp

ABSTRACT

Coevolution is one of the major drivers of complex dynamics in population ecology. Historically, antagonistic coevolution in victim-exploiter systems has been a topic of special interest, and involves traits with various genetic architectures (e.g., the number of genes involved) and effects on interactions. For example, exploiters may need to have traits that "match" those of victims for successful exploitation (i.e., a matching interaction), or traits that exceed those of victims (i.e., a difference interaction). Different models exist which are appropriate for different types of traits, including Mendelian (discrete) and quantitative (continuous) traits. For models with multiple Mendelian traits, recent studies have shown that antagonistic coevolutionary patterns that appear as matching interactions can arise due to multiple difference interactions with costs of having large trait values. Here we generalize their findings to quantitative traits and show, analogously, that the multidimensional difference interactions with costs sometimes behave qualitatively the

same as matching interactions. While previous studies in quantitative genetics have used the dichotomy between matching and difference frameworks to explore coevolutionary dynamics, we suggest that exploring multidimensional trait space is important to examine the generality of results obtained from one-dimensional traits.

Keywords: bidirectional axis of vulnerability, fluctuating selection, gene-for-gene, matching allele, unidirectional axis of vulnerability

INTRODUCTION

Theories developed from specific models are initially only as general as their underlying models, until they are shown to hold in other modeling frameworks. Hence, it is critical to compare results from a variety of modeling frameworks to test their generality. Antagonistic coevolution in victim-exploiter systems (e.g., prey-predator or host-pathogen systems) has been intensively studied theoretically (Abrams, 2000; Nuismer, 2017). It is thought to be a major driver for the emergence and maintenance of biodiversity (Thompson, 2005) and feedbacks between interacting species can create complex ecological (e.g., Cortez and Weitz, 2014) and evolutionary (e.g., Dercole et al., 2010) dynamics. Historically, various coevolution models with differing genetic architectures (e.g., the number of genes involved) and interspecific interactions (e.g., a "matching" vs. a "difference" interaction: see below) have been proposed and analyzed (Nuismer, 2017). To account for genetic architecture, one approach is to consider coevolution with a few major genes that interact and produce a discrete phenotype (Mendelian trait-based models, or hereafter Mendelian models) (e.g., Mode, 1958; Seger, 1988). On the other hand, quantitative trait-based models (hereafter quantitative models) assume the genetic architecture consists of many genes of small effect and produce continuous phenotypes (e.g., Gavrilets, 1997; Saloniemi, 1993).

Here we highlight the connection between Mendelian and quantitative models of victims and exploiters, and then clarify the relationships between existing modeling frameworks for quantitative traits. We begin by reviewing the different modeling frameworks for Mendelian traits. We then draw analogies between Mendelian and quantitative models (e.g., Boots et al., 2014; Cortez and Weitz, 2014). The analogies suggest that the matching framework, in which exploitation is more successful when traits "match" (i.e., a bidirectional axis of vulnerability *sensu* Abrams 2000), can arise from the difference framework, in which exploitation is more successful when traits differ (i.e., a unidirectional axis of vulnerability *sensu* Abrams 2000), in multidimensional quantitative models with costs of having large trait values. Finally, as a proof of concept, we give an example model of theoretical quantitative genetics where a victim-exploiter coevolutionary dynamics arising from two pairs of difference traits can appear as a matching interaction in a single pair of traits.

BACKGROUND

Historically, in Mendelian models, two major interactions were often assumed and contrasted: the matching allele (MA) framework, in which exploitation is successful when traits

61 match (e.g., Grosberg and Hart, 2000) (Figure 1a), and the gene-for-gene (GFG) framework, in
62 which a generalist exploiter can exploit a range of victim genotypes, but pays a cost for
63 generalism (Flor, 1956) (Figure 1c). Researchers have investigated the relative importance and
64 relationships of the two interactions (e.g., Agrawal and Lively, 2002; Frank, 1996; Parker, 1994).
65 Recently, Ashby and Boots (2017) found that, in multidimensional Mendelian (multilocus)
66 models, the GFG framework can behave effectively as the MA framework (Figure 2a).
67 To illustrate, consider a simple GFG model with haploid victims and exploiters with
68 two loci with two alleles each, labelled 1 and 0. The alleles 1 and 0 indicate the presence and
69 absence, respectively, of an exploitation or defense trait (Figure 2a). If both of the allelic values
70 of the exploiter are greater than or equal to those of the victim, maximum exploitation will occur
71 (black squares in Figure 2a). If the victim has exactly one allelic value greater than that of the
72 exploiter, so that the other allelic value of the victim is less than or equal to the corresponding
73 value of the exploiter, then exploitation will be partial (gray squares in Figure 2a). Finally, in the
74 case where both allelic values of the victim are strictly greater than that of the exploiter (which
75 only occurs when the victim has genotype 11 and the exploiter has 00), then the victim is
76 defended against exploitation (a white square in Figure 2a).

77 When coevolutionary dynamics occurs between four genotypes with the alleles 1 and 0,
78 the type of interaction (indicated by a dashed white line in Figure 2a) effectively reduces to a MA
79 interaction: the exploiter genotype 01 (10) is more successful at exploiting its matching counter
80 victim genotype 01 (10) as in Figure 1a. Indeed, by investigating a multilocus GFG model,
81 Ashby and Boots (2017) found that, in the case where an intermediate number of alleles is
82 optimal, the victim/exploiter genotypes alternate between various subsets of defense/exploitation
83 alleles, but the total number of alleles stays constant. Hence, the multidimensional GFG
84 framework effectively behaves as the MA framework (Figure 2a).
85 As with Mendelian models, quantitative models have assumed an apparent dichotomy
86 between two frameworks (Abrams, 2000; Abrams and Matsuda, 1997; Gilman et al., 2012;
87 McPeek, 2017): the matching trait framework, in which exploitation is increasingly more
88 successful with the extent that trait values of exploiters match those of victims (Figure 1b), and
89 the difference trait framework, in which exploitation is increasingly more successful with the
90 extent that trait values of exploiters exceed those of victims (Figure 1d). They are also known as
91 the bidirectional and unidirectional trait cases, respectively (Abrams, 2000). The matching
92 framework is analogous to the MA model and is used, for example, when an exploiter can best

93 exploit a victim with body size or color within a certain range (Brown and Vincent, 1992;
94 Calcagno et al., 2010; Dercole et al., 2010; Dieckmann et al., 1995; Fleischer et al., 2018;
95 Gavrilets, 1997; Khibnik and Kondrashov, 1997; Kopp and Gavrilets, 2006; Marrow et al., 1992;
96 Mougi, 2012; Nuismer et al., 2005; Yamamichi and Ellner, 2016). This has been observed in the
97 coevolution between the African tawny-flanked prinia and its brood parasite, the cuckoo finch:
98 the parasite varies its egg color to match that of the victim (Spottiswoode and Stevens, 2012). On
99 the other hand, the difference framework is analogous to the GFG model and is appropriate when
100 exploitation success is determined by speed vs. speed, strength vs. armor, or toxicity vs.
101 resistance (Cortez and Weitz, 2014; Frank, 1994; Mougi and Iwasa, 2010; Mougi and Iwasa,
102 2011; Northfield and Ives, 2013; Nuismer et al., 2007; Saloniemi, 1993; Sasaki and Godfray,
103 1999; Tien and Ellner, 2012; van Velzen and Gaedke, 2017; Yamamichi and Miner, 2015). For
104 example, garter snakes evolve stronger resistance to rough-skinned newt toxicity in areas where
105 newts are more toxic (Brodie III and Brodie Jr, 1990).
106 In the matching framework, exploitation success is typically a unimodal function of the
107 trait difference, and is often modeled as a Gaussian: $\exp[-(x-y)^2]$, where x and y are traits of
108 victims and exploiters, respectively (Figure 1b) (e.g., Gavrilets, 1997; Khibnik and Kondrashov,

1997; Mougi, 2012; Nuismer et al., 2005). On the other hand, in the difference framework, exploitation success is often modeled as a sigmoidal function of the trait difference: $1/[1 + \exp(x - y)]$ (Figure 1d) (e.g., Mougi and Iwasa, 2010; Nuismer et al., 2007; van Velzen and Gaedke, 2017). In this framework, it is always advantageous for both species to increase the trait values for better exploitation/defense (McPeek, 2017). Empirical evidence suggests that there is an energetic trade-off to exploitation and defense and hence, most models of difference traits assume there is a cost associated with each trait, which prevents runaway evolution. For example, garter snakes resistant to newt toxin have costs associated with slower sprinting speeds (Brodie III and Brodie Jr, 1999), milkweed bugs' production of enzymes to break down milkweed toxins has metabolic costs (Dalla and Dobler, 2016), and numerous plants produce defense chemicals with a cost to plant growth (reviewed in Herms and Mattson, 1992).

Here, by drawing analogies between the Mendelian trait and quantitative trait frameworks (Figure 1), we further extend the generalization of Ashby and Boots (2017) and demonstrate that the difference framework can result in similar dynamics to the matching framework in multidimensional quantitative models. The matching model is a continuous trait analog to the MA model and the difference model is a continuous trait analog to the GFG model

125 (Figure 1). In a multilocus GFG model, under certain conditions the victim/exploiter genotypes
126 alternate between various subsets of defense/exploitation alleles, but the total number of alleles
127 stays constant, which is effectively what occurs under the MA framework (Ashby & Boots 2017).
128 This is analogous to a bivariate difference trait model, in which the victim/exploiter genotypes
129 alternate between having more investment in one defense/exploitation trait vs. another, which is
130 effectively what occurs under the matching framework. Instead of switching between the
131 extremes of a single matching trait, the species are switching between two difference-trait-based
132 strategies. We consider a victim-exploiter model in which each has two difference traits that
133 influence exploitation success. An empirical example that motivates our study is a stepwise
134 infection process (Hall et al., 2017), where host species prevent exploitation of parasites by
135 several difference traits. In the case where intermediate trait values are optimal due to the costs of
136 defense/offense, the victim/exploiter traits may switch between combinations where a trait is
137 large while the other trait is small, but the total costs stay constant. The resultant dynamics may
138 appear as the matching interaction, and this is the quantitative-model analog to the findings in
139 Ashby and Boots (2017) in Mendelian models.
140

AN EXAMPLE

We develop a two-dimensional quantitative model with difference interactions (Figure 2b) to demonstrate that matching dynamics can emerge from a multidimensional difference framework (see Appendix S1 and Supplementary Mathematica file, Supporting Information, for details). We consider a quantitative genetic model (Iwasa et al., 1991; Lande, 1976) in continuous time (i.e., Malthusian fitness) (Abrams et al., 1993). We assume that victims and exploiters each have two quantitative traits. We let x_i be the value of victim trait i (= 1, 2) and assume greater values allow for defense against trait i of the exploiter. We let y_i be the value of exploiter trait i and assume greater values allow for more exploitation. Each trait is associated with a cost that decreases individual fitness with greater trait values. The difference between the exploiter trait and the corresponding victim trait, $y_i - x_i$, affects exploitation success (Figure 2b), which is expressed by a sigmoid function (Figure 1d). We assume that fitness of victims and exploiters are, respectively,

$$\begin{aligned} m_x &= r\left(x_1, x_2\right) - a_0 \prod_{i=1}^{2} \frac{1}{1+\exp\left[-\theta_i\left(y_i - x_i\right)\right]}, \\ m_y &= c\left(y_1, y_2\right) a_0 \prod_{i=1}^{2} \frac{1}{1+\exp\left[-\theta_i\left(y_i - x_i\right)\right]}, \end{aligned} \tag{1}$$

where a_0 is the effects of successful exploitation on fitness (e.g., maximum attacking rate), and θ_i (i = 1, 2) determine the sensitivity of exploitation success to the trait difference. In our model, the product $\prod_{i=1}^{2} 1 \Big/ \left\{1+\exp\left[-\theta_i\left(y_i - x_i\right)\right]\right\}$ means that victims need to overcome their exploiters at only one trait for escaping from exploitation, whereas exploiters must overcome the two defense traits for successful exploitation (Gilman et al. 2012). This sequential interaction is also found in many host-parasite systems (Hall et al. 2017).

Here r and c represent costs of defense and exploitation for victims and exploiters, respectively (e.g., prey growth and predator conversion efficiency are decreasing functions of defense and offense, respectively: see Appendix S1, Supporting Information), and they are linearly decreasing functions of the sum of the two traits values (i.e., lower values of r and c represent higher costs). The costs can prevent escalation toward positive infinite values in the two traits. However, the two-dimensional difference model with costs behaves like a one-dimensional matching model, in which runaway evolution occurs toward a positive infinite value in one trait and a negative infinite value in the other trait (Appendices S2, S3, Figures S1, S2, Supporting Information). To prevent this, we add stabilizing selection to the victim cost function as in

Gavrilets (1997). This can occur in quantitative models but not in Mendelian models because it is customary to assume unbounded trait values in quantitative models, which permits the existence of runaway escalation, whereas Mendelian traits are typically modeled as taking values in finite sets. We employ the following functions:

$$
\begin{aligned}
r &= r_0\left(1-\sum_{i=1}^{2}\rho_{xi}x_i\right)\exp\left[-\sum_{i=1}^{2}s_i\left(x_i-x_{i0}\right)^2\right],\\
c &= c_0\left(1-\sum_{i=1}^{2}\rho_{yi}y_i\right),
\end{aligned}
\tag{2}
$$

where r_0 and c_0 are basic parameter values (e.g., for prey growth rate and predator conversion efficiency) and ρ_{ij} ($i = x, y, j = 1, 2$) determine the slope of the functions. Stabilizing selection drives victim evolution toward $(x_1, x_2) = (x_{10}, x_{20})$, where s_i ($i = 1, 2$) determines the strength of stabilizing selection (Figure S3, Supporting Information). Note that adding stabilizing selection to the exploiter function instead of the victim function results in victim's escape from exploitation. We can add stabilizing selection to the exploiter function in addition to the victim function, but here we keep the model as simple as possible.

Then coevolutionary dynamics are described by four ordinary differential equations,

$$\frac{d}{dt}\begin{pmatrix} x_1 \\ x_2 \end{pmatrix} = \begin{pmatrix} v_{x11} & v_{x12} \\ v_{x12} & v_{x22} \end{pmatrix} \begin{pmatrix} \frac{\partial m_x}{\partial x_1} \\ \frac{\partial m_x}{\partial x_2} \end{pmatrix},$$

$$\frac{d}{dt}\begin{pmatrix} y_1 \\ y_2 \end{pmatrix} = \begin{pmatrix} v_{y11} & v_{y12} \\ v_{y12} & v_{y22} \end{pmatrix} \begin{pmatrix} \frac{\partial m_y}{\partial y_1} \\ \frac{\partial m_y}{\partial y_2} \end{pmatrix}, \quad (3)$$

where v_{ijj} ($i = x, y, j = 1, 2$) represents additive genetic variance, v_{i12} ($i = x, y$) represents covariance, and partial derivatives represent fitness gradients (Abrams et al., 1993). For simplicity, we assume that the traits evolve independently (genetic covariance, v_{i12}, is zero). For example, this is likely in hosts that defend against parasites by a cellular immune response and a behavioral response, but further work is needed to explore the effects of trait correlations. Also, our trait symmetry assumptions (i.e., the additive genetic variances are the same, $v_{i11} = v_{i22}$, and the two traits affect exploitation success and fitness costs in the same way, $\theta_1 = \theta_2$, $\rho_{x1} = \rho_{x2}$, $\rho_{y1} = \rho_{y2}$, and $s_1 = s_2$) should be carefully examined in future studies as this assumption may not hold for most traits (Figure S4, Supporting Information), and it may result in, for example, time-scale separation in evolutionary dynamics of the two traits.

By numerically solving the model, we find that the two-dimensional difference model can behave as a one-dimensional matching model. First, when there is no stabilizing selection in the victim cost ($s_i = 0$) and the exploiter genetic variance is small enough ($v_{xii} >> v_{yii}$, $i = 1, 2$), coevolutionary dynamics shows runaway escalation toward extreme trait values, and the coevolutionary outcome depends on initial conditions (Figure S2, Supporting Information). Second, when there is stabilizing selection ($s_i > 0$) and the exploiter genetic variance is large enough (e.g., $v_{xii} < v_{yii}$), the system is attracted to a stable equilibrium (the blue and red points in Figures 3a, 3b), and there is disruptive selection for victim traits (i.e., fitness minimum: vectors representing fitness gradients in Figure 3a are distracted from the equilibrium) and stabilizing selection for exploiter traits (i.e., fitness maximum: vectors in Figure 3b are attracted to the equilibrium), which is consistent with the matching interaction (Appendix S2, Supporting Information) (Abrams and Matsuda, 1997; Gavrilets, 1997). Third, when there is stabilizing selection ($s_i > 0$) and the exploiter genetic variance is small enough ($v_{xii} >> v_{yii}$), the equilibrium is not stable (Appendix S3, Figure S3, Supporting Information) and the trait dynamics fluctuate (Figure 3c) but are constrained to regions in which the total investments are nearly constant (Figure 3d) and the two traits for each species show antiphase cycles (Figures 3c, 3e, 3f). These

simulation results demonstrate that the matching dynamics can arise from the difference interaction, generalizing Ashby and Boots (2017)'s idea from Mendelian models to quantitative models.

DISCUSSION

Victim-exploiter interactions are among the most fundamental type of ecological interactions. In addition to their importance in ecological communities, these interactions are widely recognized for playing an important role in ecological dynamics (e.g., extinction and predator-prey cycles: Cortez and Weitz (2014); Northfield and Ives (2013)) and evolutionary dynamics (e.g., sex, recombination, and epistasis: Otto and Lenormand (2002)), because each species needs to continue to adapt to new selection pressures by the other species. Due to its importance, many modeling frameworks have been proposed to investigate the dynamics of coevolution between a victim and its exploiter, capturing various aspects of the traits involved (Nuismer, 2017).

In this work, we highlight the relationship between two modeling frameworks of quantitative traits in victim-exploiter coevolution. In particular, a multidimensional difference

trait framework, in which each trait confers an advantage in the victim-exploiter interaction but is associated with some cost (Figures 1d, 2b) can generate dynamics like a matching trait framework, in which traits between a victim and exploiter must "match" in some sense for successful interactions (Figure 1b). Our investigation extends our knowledge of the coevolutionary process by demonstrating how effectively matching dynamics can be generated from difference traits with costs in a special case of multivariate coevolution as a proof of concept (rather than a thorough investigation of the dynamics: Figure 3).

For some traits, the distinction between matching traits and difference traits is clear. For both victims and exploiters, being stronger and faster are always more advantageous (but may have an associated cost or energetic limitation) and hence, are difference traits. However, in other cases, it is not so obvious. For example, body size of both victims and exploiters can be a difference trait, in which bigger is better for exploitation/defense (e.g., gape-limited predation), or a matching trait, in which exploiters must be within a certain size range depending on victims' size for successful exploitation. Besides classifying difference vs. matching traits, a second empirical difficulty arises when not all traits are simultaneously measured. Our simulations suggest that, even when the body size is a difference trait, it may behave as a matching trait

248 because of another potentially unmeasured difference trait such as toxicity/resistance. This
249 correlated coevolution between the two traits can occur even without genetic covariance, as long
250 as the body size and toxicity/resistance affect exploitation success and the costs of being big
251 affect fitness together with the costs of the toxicity/resistance.

252 Previous work has suggested that matching traits are more likely to lead to
253 coevolutionary cycling of traits than difference interactions (Abrams, 2000; McPeek, 2017). In
254 comparing quantitative models with a one-dimensional trait, for example, McPeek (2017) found
255 cycles are observed in a smaller area of parameter space with difference traits compared to
256 matching traits. Furthermore, the underlying mechanism of cycles differs in the two frameworks.
257 In the matching framework, cycles consist of the exploiter tracking victim traits and the victim
258 escaping from exploiter traits (i.e., fluctuating selection between equally specific
259 defense/exploitation traits). In the difference framework, cycles consist of the victim and
260 exploiter investing more energy in their traits for better defense/exploitation, and then
261 abandoning their defense/exploitation because at some point they are too costly to maintain (i.e.,
262 fluctuating selection between strong and weak defense/exploitation traits). Even when empirical
263 researchers are focusing on a single trait with the difference interaction, the system may have

264 another difference trait that can affect exploitation success. In such a case, coevolutionary
265 dynamics can be driven by the matching-like interaction, which may cause cyclic dynamics more
266 easily (McPeek, 2017).

267 In spite of recent interest in coevolution in multidimensional trait space (e.g., Débarre
268 et al., 2014; Doebeli and Ispolatov, 2017; Gilman et al., 2012), the relation of the matching and
269 difference frameworks has not been well recognized. For example, in their study on evolutionary
270 escape, Gilman et al. (2012) contrasted coevolutionary dynamics with matching and difference
271 interactions in multidimensional trait space but did not find a significant difference between them
272 (see Figure 1 of Gilman et al. (2012)). Our generalization offers a potential explanation for this
273 previous work, as coevolutionary dynamics with matching interactions can arise from difference
274 interactions in multidimensional quantitative models.

275 This work was inspired by the recent work of Ashby and Boots (2017), who showed an
276 analogous relationship for two Mendelian trait models of coevolution. Here, we draw out the
277 parallels between two Mendelian (single-locus) trait frameworks and two quantitative trait
278 frameworks. Namely, we highlight that the matching allele (MA) framework is a Mendelian
279 analog of the matching framework, and the gene-for-gene (GFG) framework is a Mendelian

analog of the difference framework (Figure 1). While these frameworks are valuable, many traits important to victim-exploiter interactions may actually lie somewhere in the middle of these two extremes; they may be determined by many (but not infinite number of) loci. It is still not well understood how coevolutionary dynamics differ between when traits are governed by a single locus, multi-locus (with linkage disequilibrium and epistasis), and effectively infinite loci (as assumed in classical quantitative genetics). While there have been a handful of papers to investigate this question in specific scenarios, further investigation is need for a general understanding.

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421 **FIGURE LEGENDS**

422 **FIGURE 1.** Interaction frameworks and genetic architectures in coevolution models. (a)
423 Matching allele (MA) is a matching interaction in Mendelian traits. Victims and exploiters are
424 haploid and their genotypes are represented by 1 and 0 at a particular locus. Dark shading
425 indicates greater exploitation success. (b) The matching interaction is a MA interaction in
426 quantitative traits. Exploitation success is maximized when the trait difference is zero. (c)
427 Gene-for-gene (GFG) is a difference interaction in Mendelian traits. Here 1 and 0 indicate the
428 presence and absence, respectively, of defense/exploitation alleles. (d) The difference interaction
429 is a GFG interaction in quantitative traits. Exploitation success is increased by larger exploiter
430 trait values and by smaller victim trait values.

431

432 **FIGURE 2.** (a) An example of exploitation matrix in a Mendelian GFG model with two loci
433 (Ashby and Boots, 2017). The region surrounded by a dashed white line shows that the MA
434 interaction arises from the GFG framework. Victims and exploiters are haploid and their
435 genotypes are represented by 1 and 0 at a locus, and they indicate the presence and absence,
436 respectively, of defense/exploitation alleles. Darker shading indicates greater exploitation success

437 and arrows indicate greater costs. (b) Exploitation success as a function of both trait differences

438 between exploiters and victims ($y_i - x_i$) in a quantitative difference model with two traits

439 (Equation 1).

440

441 **FIGURE 3.** Coevolutionary dynamics of two quantitative traits with difference interactions. (a,

442 b) Fitness landscapes of victims (a) and exploiters (b) when the exploiter genetic variance is large

443 enough and the system converges to a stable equilibrium. (a) A contour plot of fitness (m_x) and a

444 vector field of fitness gradients for the victim traits when the exploiter traits are at the equilibrium

445 trait value (the red point in b). (b) A contour plot of fitness (m_y) and a vector field of fitness

446 gradients for the exploiter traits when the victim traits are at the equilibrium trait value (the blue

447 point in a). Parameter values are $\rho_{xi} = 0.07$, $\rho_{yi} = 2$, $x_{10} = x_{20} = 0.2$, $a_0 = r_0 = c_0 = \theta_i = v_{jii} = 1$, $s_i =$

448 0.01, and $v_{j12} = 0$ ($i = 1, 2, j = x, y$). (c-f) Coevolutionary cycles when the victim genetic variance

449 is much larger than exploiter genetic variance ($v_{xii} >> v_{yii}$). (c) Numerical solutions of the four

450 traits. (d) Numerical solutions of the functions (Equation 2) representing costs of

451 defense/exploitation (note that lower values indicate higher costs). (e, f) Coevolutionary cycles of

452 victims (e) and exploiters (f). Parameter values are the same as (a) and (b) except for $v_{xii} = 1$ and

$v_{yii} = 0.01$ ($i = 1, 2$). Note that c is negative in gray regions in (b) and (f).

Figure 1.

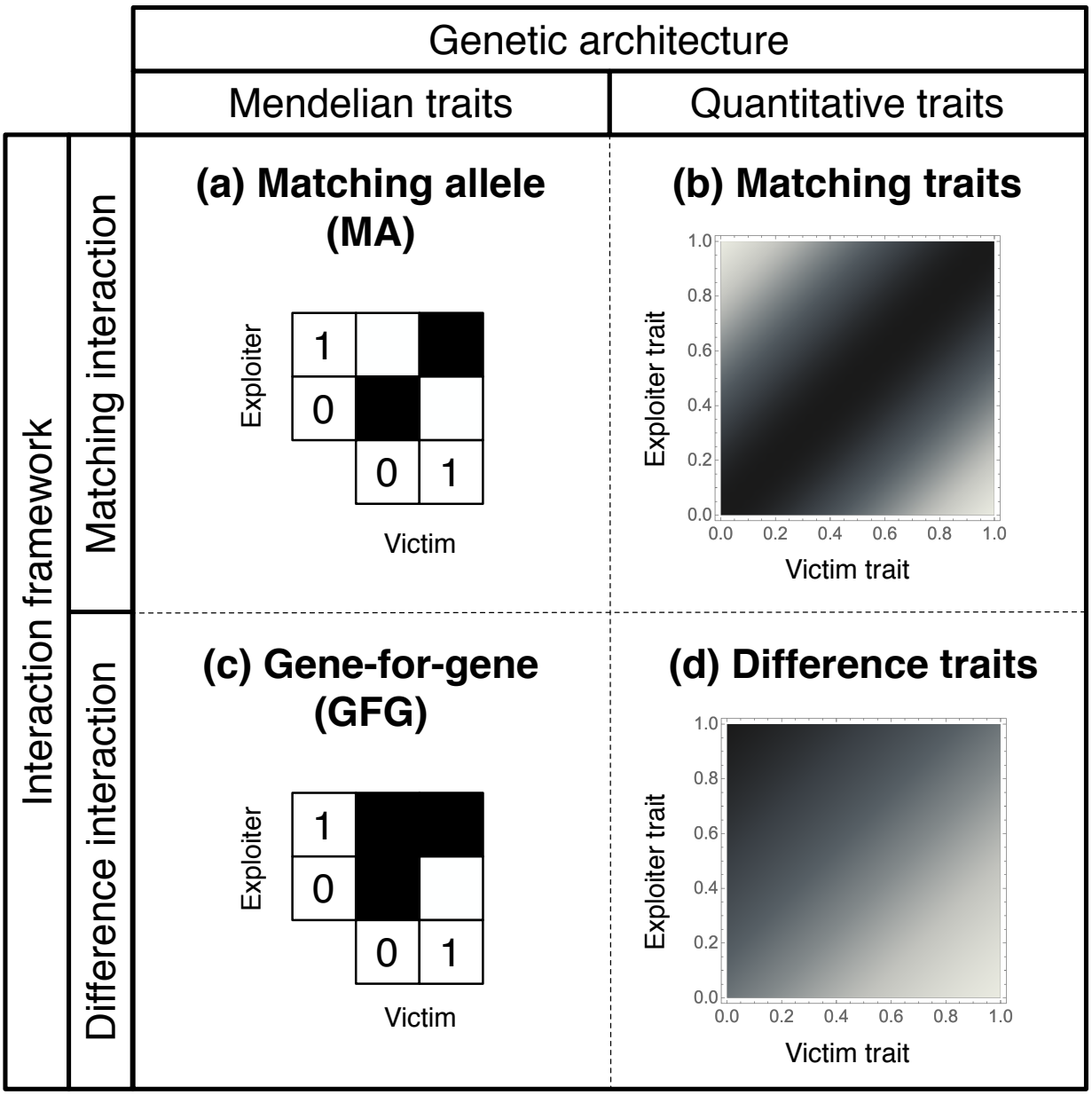

Genetic architecture
Mendelian traits
Quantitative traits
Interaction framework
Matching interaction
Difference interaction
(a) Matching allele (MA)
Exploiter
1
0
0
1
Victim
(b) Matching traits
Exploiter trait
Victim trait
0.0
0.2
0.4
0.6
0.8
1.0
(c) Gene-for-gene (GFG)
Exploiter
1
0
0
1
Victim
(d) Difference traits
Exploiter trait
Victim trait
0.0
0.2
0.4
0.6
0.8
1.0

Figure 2.

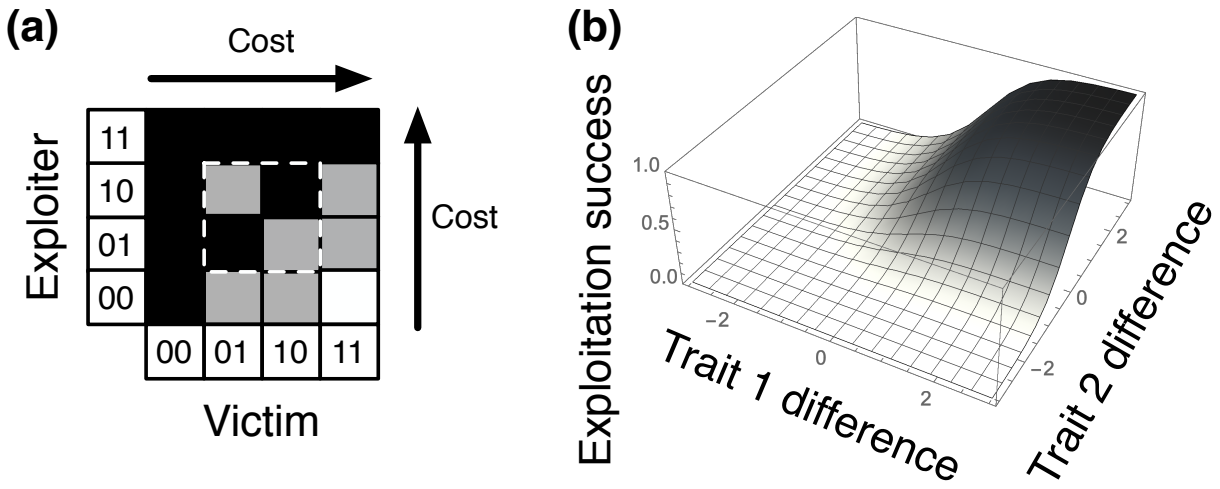
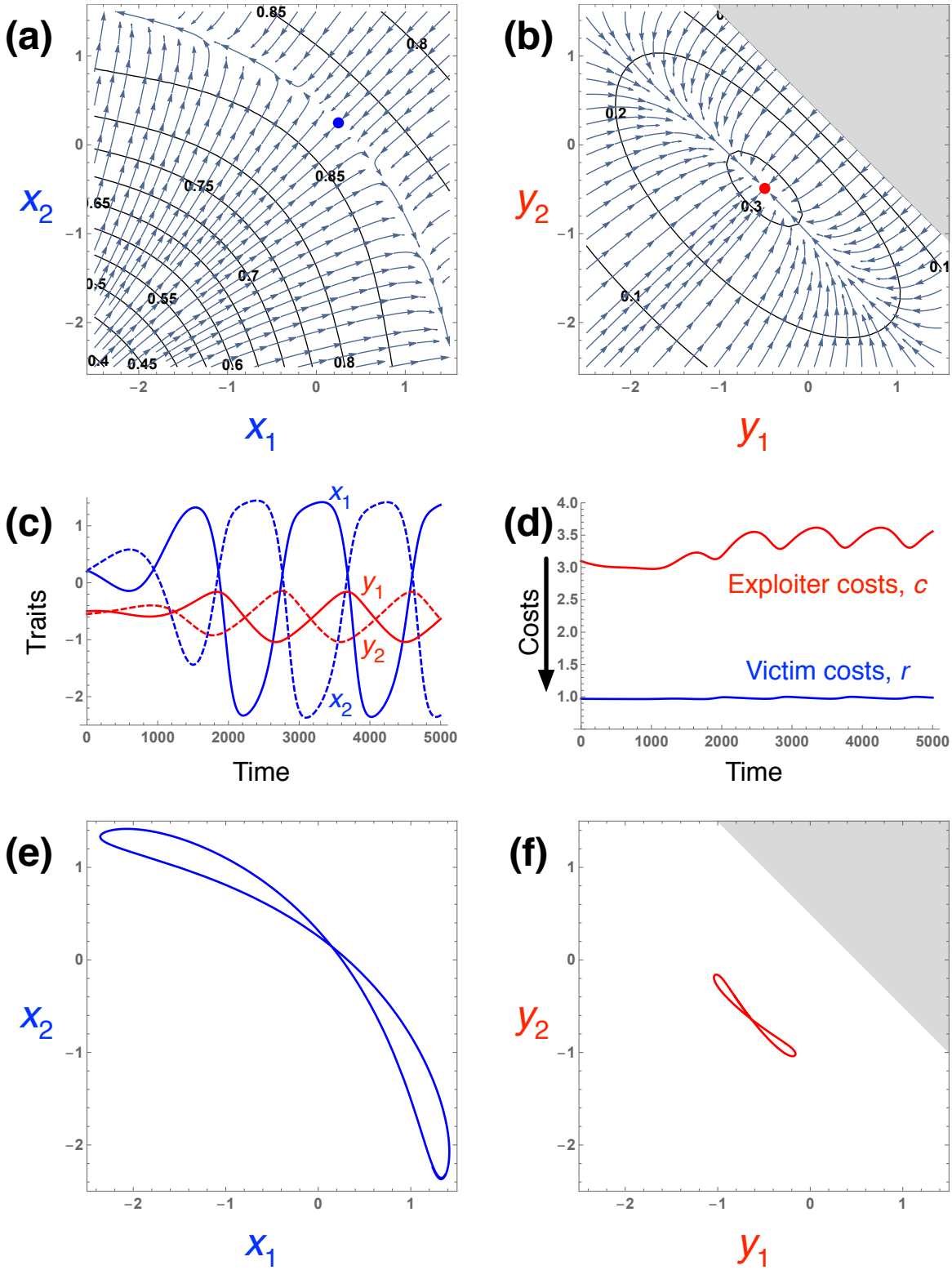

(a)
Cost
Cost
Exploiter
11
10
01
00
00
01
10
11
Victim
(b)
Exploitation success
1.0
0.5
0.0
−2
0
2
Trait 1 difference
2
0
−2
Trait 2 difference

Figure 3.


(a)
(b)
(c)
(d)
(e)
(f)
x_1
x_2
y_1
y_2
Traits
Time
Costs
Exploiter costs, c
Victim costs, r